CellPress
REVIEWS

Opinion

Experiments Are Necessary in Process-Based Tree Phenology Modelling

Heikki Hänninen,[1,5,*] Koen Kramer,[2,5] Karen Tanino,[3] Rui Zhang,[1] Jiasheng Wu,[1] and Yongshuo H. Fu[4]

In boreal and temperate trees, air temperature is a major environmental factor regulating the timing of spring phenological events, such as vegetative bud burst, through underlying physiological processes. This has been established by experimental research, and mathematical process-based tree phenology models have been developed based on the results. The models have often been applied when assessing the effects of climate change. Currently, there is an increasing trend to develop process-based tree phenology models using only observational phenological records from natural conditions. We point out that this method runs a high risk of producing models that do not simulate the real physiological processes in the trees and discuss experimental designs facilitating the development of biologically realistic process-based models for tree spring phenology.

Spring Phenology: An Essential Aspect of Tree and Forest Ecology

Timing of vegetative bud burst and other spring phenological events is crucial in the climatic adaptation of boreal and temperate trees. A trade-off in the timing occurs because a premature bud burst early in the spring increases the risk of damage by late frosts, while a delayed bud burst late in the spring causes a partial loss of the growing season [1,2]. Changes in spring tree **phenology** (see Glossary) have major implications for crucial ecological phenomena, ranging from carbon sequestration of the forest ecosystem [3–5] to the synchronisation of the phenological timing of the trees with that of animals [6,7]. The ecological implications often have further economic implications because many of the boreal and temperate tree species are important in practical forestry or horticulture [8]. During the past couple of decades, scientific interest in spring tree phenology has increased dramatically due to climatic change [9]. Advancing of spring phenological events has been generally observed as a result of climate warming [10–13]. However, this effect is often counteracted by reduced **chilling** [14–18], which may, under some circumstances, cause a delay of the spring phenological events [19]. Future changes in tree spring phenology are often projected by using mathematical tree phenology models in scenario computer simulations [2,20,21]. In this opinion article, we show that more experimental research designed for developing and testing the models used in the simulations is needed to increase their biological realism and the trustworthiness of the projections obtained with them.

Process-Based Modelling of Tree Spring Phenology

The main ecophysiological processes involved in the regulation of spring phenology in boreal and temperate trees are, in broad terms, relatively well understood, even though several uncertainties still prevail ([2,22] and the references therein). Air temperature plays a dual role in regulating the timing of the spring phenological events, such as vegetative bud burst, or flowering (Figure 1). First, after growth cessation and bud set in late summer or early autumn,

Highlights

Studies addressing spring phenology of trees are increasingly topical because of the ongoing climate change.

Spring phenology of trees is often studied with process-based mathematical models, which simulate physiological processes underlying the timing of phenological events, such as vegetative bud burst.

Process-based tree phenology models are often used in computer simulations for projecting the effects of future climate warming on trees and forest ecosystems.

Traditionally models have been developed with the aid of growth chamber and greenhouse experiments, which have facilitated the determination of environmental responses of the physiological processes. However, nowadays models are often developed without experimental research, using observational long-term phenological records, or remote-sensed data, gathered in natural conditions as the only biological information.

[1]Zhejiang A&F University, State Key Laboratory of Subtropical Silviculture, Hangzhou, China
[2]Wageningen Environmental Research, Wageningen University and Research, Wageningen, The Netherlands
[3]University of Saskatchewan, Department of Plant Sciences, Saskatoon, Canada
[4]Beijing Normal University, College of Water Sciences, Beijing 100875, China
[5]These authors contributed equally to this work

*Correspondence:
hhannin@zafu.edu.cn (H. Hänninen).
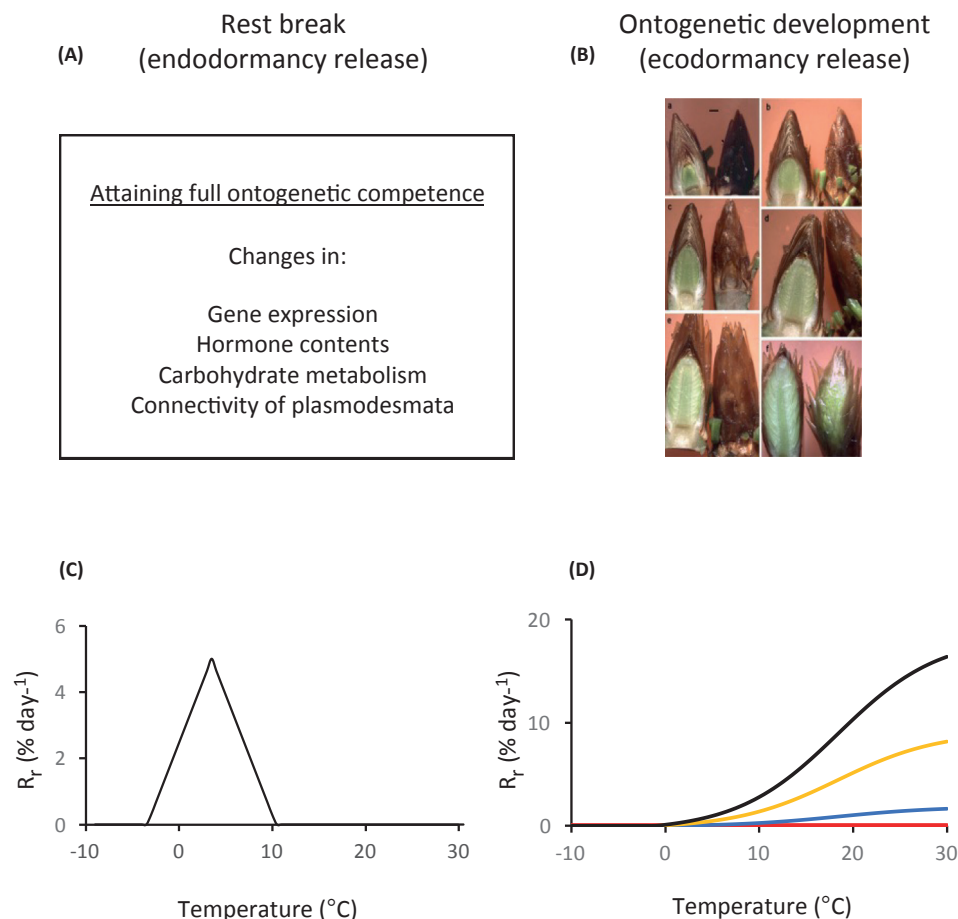
Figure 1. (A,B) Physiological Processes and (C,D) their Air Temperature Responses Addressed in Process-Based Modelling of Tree Spring Phenology. R_r = rate of rest break, R_o = rate of ontogenetic development towards bud burst. Rest break is driven by chilling temperatures and ontogenetic development by high forcing temperatures. During rest break, physiological growth-arresting conditions inside the bud are removed. That leads to increasing ontogenetic competence of the buds, so that R_o in any given forcing temperature increases. In the parallel model, R_o increases gradually, as shown by the four curves with different colours in (D). In the sequential model, R_o increases abruptly from zero in any temperature (red curve) to the full rate (black curve) at the time of meeting the chilling requirement of rest completion [2]. In addition to chilling temperatures, night length affects rest break in some tree species, but for the sake of simplicity this is not shown in the figure. Photos by Sirkka Sutinen and Seija Repo.

long-term (days to months) exposure to low **chilling temperatures** is required for **rest break** (or endodormancy release [23]). During rest break, growth-arresting physiological conditions in the buds are removed, so that the buds attain full **ontogenetic competence**, that is, the full ability to respond to high **forcing temperatures** by anatomic development towards bud burst (Figure 1A,C). The **chilling requirement of rest completion** varies among tree species, provenances, and even individuals [2,24,25]. In some tree species, especially *Fagus sylvatica*, night length (or photoperiod) also plays a role in the rest break [26–29]. Although the **rest** period and the chilling requirement of rest completion have been known on the whole tree level for almost 100 years [30], their molecular and physiological basis remains still only partially understood, despite recent advances in this research field [31–34].

Glossary

Chilling: exposure of the bud to chilling temperatures.
Chilling requirement of rest completion: the duration of chilling required for rest completion. The duration often depends on the chilling temperature.
Chilling temperature: any temperature causing rest break in the buds. Exact temperature range depends on the species studied. Usually temperatures a few degrees below and above +5°C are most effective as chilling temperatures.
Dormancy: the state when no visible growth or bud burst is observed in an overwintering bud of a tree, regardless of the reason for the inactivity.
Dynamic model: a mathematical model simulating the progress of a process over time.
Forcing temperature: any temperature above a specific threshold causing ontogenetic development towards bud burst. The threshold depends on the tree species.
High temperature requirement of bud burst: the duration of forcing temperature exposure required for bud burst. The duration depends on the forcing temperature.
Inverse modelling: in this study, a technique where process-based tree phenology models are developed based on observational data of air temperature and timing of bud burst in natural conditions. More generally, a modelling technique where the cause is inferred from the effect.
Model accuracy: the degree to which the predictions of a model fit observations.
Model realism: the degree to which the relationships described by a model correspond to real ecophysiological relationships in real trees.
Ontogenetic competence: a relative quantitative measure of the bud's ability to respond to high forcing temperatures by microscopic anatomical development towards bud burst. With zero ontogenetic competence no such development takes place (red curve in Figure 1D), whereas with full ontogenetic competence the development progresses at the maximum rate in

At the time of **rest completion**, the period of **quiescence** (or ecodormancy [23]) is attained. During quiescence, microscopic development towards the visible phenological event occurs in the buds as a result of high forcing temperatures above a given threshold (Figure 1B,D). For the sake of brevity, the microscopic processes taking place in the buds will be referred to below as **ontogenetic development** [2,35]. Finally, as a result of a long-term (days to months) exposure to the forcing temperatures, ontogenetic development leads to the occurrence of the visible phenological event, such as bud burst [36–38]. Similar to the chilling requirement of rest completion, the **high temperature requirement of bud burst** varies among tree species, provenances, and even individuals [2,24,39].

Based on experimental work, **process-based models** have been developed since the early 1970s for rest break and ontogenetic development of boreal and temperate trees (Figure 1) [35,40,41]. More recently, these models have been frequently used for assessing the ecological implications of climate change [2,20,21]. The process-based spring phenology models belong to the category of **dynamic models**, simulating the progress of the addressed processes over time. The **rate of rest break** and **rate of ontogenetic development** are first calculated for a short time interval, say 1 day, based on the temperature prevailing during the time interval (Figure 1C,D). Subsequently, the **state of rest break** and **state of ontogenetic development** are obtained by integrating the corresponding rates with respect to time, that is, by summing the daily values of the corresponding rate variable [42]. In addition to the prevailing air temperature, the rate of ontogenetic development is also regulated by the state of rest break, that is, the degree to which the chilling requirement is fulfilled. Two main alternatives, the **sequential model** and the **parallel model**, have been proposed for this regulation. Both of them, and any intermediate model between them, can be addressed with a variable quantifying the ontogenetic competence, that is, the ability of the bud to react to the forcing temperatures by showing ontogenetic development (Figure 1) [2,24,40].

The mathematical formulation of the process-based tree phenology models varies among published models, but ecophysiologically, all comprehensive models describe the two processes, rest break and ontogenetic development, with their respective two submodels (simplified models addressing only the ontogenetic development are outside the scope of the study). A third submodel is needed for the dependence of the ontogenetic competence on the state of rest break, that is, for describing the effects of the first process (rest break) on the second one (ontogenetic development) [40]. The crucial question is how the three submodels can be formulated to realistically describe the causal relationships involved in the particular tree species and provenance.

Inverse Modelling: An Unsuccessful Attempt for a Shortcut

Since the mid-1990s, the **inverse modelling** technique [43] has been applied in process-based tree phenology modelling. Inverse modelling applied to phenological studies takes observational data for air temperature and timing of phenological events, such as bud burst, as input and then uses numerical search techniques to derive parameter values for air temperature (and night length) responses of rest break and ontogenetic development (Figure 1C,D). In addition to classical phenological records, remote-sensed data has been applied in these studies (Table 1). The process-based phenological model with the best fit for the observed and modelled timing of the phenological events is then selected [44–47].

The reason for the current popularity of the inverse modelling technique is obvious: this approach is straightforward to implement because large, long-term data sets of the phenological records are now available for several tree species, even as open access resources (http://

each temperature (black curve in Figure 1D).

Ontogenetic development: in this study, the microscopic anatomical development inside the bud, leading to the visible bud burst. More generally, the irreversible development of any biological structure.

Parallel model: a model assuming that ontogenetic development already takes place during rest period in forcing temperatures, but the rate of development is lower than during quiescence.

Phenology: study of the timing of seasonally recurring developmental phenomena, such as vegetative bud burst of trees during spring.

Process-based model: a computer model addressing explicitly the physiological processes affecting a given phenomenon being observed at the whole-tree level, such as bud burst.

Quiescence: a phase of dormancy when the growth onset is prevented by unfavourable environmental conditions of the tree, usually low temperatures. Ontogenetic development towards visible bud burst occurs whenever air temperature rises above the forcing temperature threshold. Synonymous to ecodormancy.

Rate of ontogenetic development: R_o, a model variable showing the percentage of the ontogenetic development towards bud burst taking place during 1 day (Figure 1D).

Rate of rest break: R_r, a model variable showing the percentage of the processes of rest break required for rest completion taking place during 1 day (Figure 1C).

Rest: a phase of dormancy when the growth onset is prevented by physiological factors inside the bud. Synonymous to endodormancy.

Rest break: the process of removing the internal growth-arresting physiological conditions in the bud.

Rest completion: the event during dormancy when the internal growth-arresting physiological conditions are entirely removed in the bud.

Sequential model: a model assuming that ontogenetic development takes place only after rest completion.

www.pep725.eu; [56]). By contrast, the experimental work, especially when conducted at the microscopic and physiological levels, needs much more research effort. Furthermore, as the inverse modelling is based on observations under natural conditions, it is not vulnerable to the artefacts often hampering experimental studies [57].

However, despite the high accuracy often obtained with inverse modelling, the inverse modelling approach is seriously vulnerable to producing models of low realism, that is, models which do not describe the real physiological processes taking place in the real trees (for a discussion of **model accuracy** versus **model realism**, see Levins [58,59], Sharpe [60], and Hänninen [2]). Hunter and Lechowicz [61] were the first to point out the problem. They generated artificial data sets of the spring phenological event by the process-based models, thus assuming that the particular model used in the generation of the data represents the real environmental responses of rest break and ontogenetic development. Subsequently, they demonstrated that several other models, in addition to the 'realistic' one used in generating the artificial data, were equally able to fit the generated observations.

The pivotal study of Hunter and Lechowicz [61] showed that model fitting with the inverse modelling using solely observational phenological records is unable to identify the realistic process-based phenological model among several competing ones. The inverse modelling may produce the realistic model, but the major problem is that there is no way to evaluate this. This conclusion has been confirmed in later studies using measured phenological data [20,44,45,49,51]. Furthermore, even an experimental approach does not guarantee the identification of the realistic model, if the experiment is not specifically designed for testing the competing phenological models. This was shown in a study where 96 competing process-based phenological models were tested with *Pinus sylvestris* saplings in a whole-tree chamber experiment simulating climate warming and thus using natural night length [62]. In the test, a model that assumed night length regulates the rest break in the *P. sylvestris* saplings was the most accurate. However, in a simultaneous experiment specifically designed for testing the night length model under controlled night length conditions in the same sapling population, night length had no influence on the rest break. This shows that despite its high accuracy in the whole-tree chamber experiment with natural night length, the photoperiod model did not have any biological realism whatsoever in the case of those saplings studied [62].

In all of the cases discussed above, the lack of biological realism is a result of the inability of the observational phenological records to derive information on the underlying physiological processes [2]. In inverse modelling, the processes are not actually examined at all, as only bud burst in spring is observed. Despite that, similar to the experimentally based models, the models developed with inverse modelling are applied in computer simulations lasting from the autumn to the spring [20,21,50]. This severely undermines the trustworthiness of studies where the ecological effects of climate change are assessed with the process-based tree phenology models [2].

Recently, Chen *et al.* [21] used inverse modelling in studying the spring phenology of *Melia azedarach* in subtropical and tropical conditions in southeastern China. The tree species is of tropical origin, and as far as we know, there are no experimental studies establishing the existence of rest period, let alone that of chilling requirement, for any native subtropical or tropical tree species. In other words, Chen *et al.* [21] modelled tree physiological phenomena without any evidence of the existence of those phenomena in the real trees. This is a striking example of how the research tradition applying the inverse modelling is losing its connection to the experimental tradition that has originally provided both the conceptual framework and the empirical evidence for the process-based tree phenology modelling.

State of ontogenetic development: a model variable showing the percentage of the ontogenetic development towards bud burst having taken place at a given moment. It is obtained by summing the previous daily values of the rate of ontogenetic development (Figure 1D).

State of rest break: a model variable showing the percentage of the processes of rest break required for rest completion having taken place at a given moment. It is obtained by summing the previous daily values of rate of rest break (Figure 1C).

Table 1. Examples of Studies Using Inverse Modelling in Process-Based Tree Phenology Modelling Since Introducing the Approach in 1994 Until the Present

Publishing year	Tree species	Phenological event	Climatic zone	Refs
1994	*Fagus sylvatica*	Leaf unfolding	Temperate	[44]
1994	*Betula pubescens, F. sylvatica, Fraxinus excelsior, Larix decidua, Picea abies, Pinus sylvestris, Quercus petraea, Quercus robur, Quercus rubra, Tilia cordata, Tilia platyphylla*	Leaf unfolding	Temperate	[45]
1998	*Aesculus hippocastanum, Alnus glutinosa, Buxus sempervirens, Olea europaea, Platanus acerifolia, Taxus baccata, Ulmus minor*	Flowering	Temperate	[46]
1999	*A. hippocastanum, A. glutinosa, Betula verrucosa, B. sempervirens, Carpinus betulus, Castanea sativa, Corylus avellana, O. europaea, P. acerifolia, T. baccata, U. minor, Ulmus montana*	Flowering	Temperate	[47]
2000	*A. hippocastanum, B. sempervirens, O. europaea, P. acerifolia, T. baccata, U. minor*	Flowering	Temperate	[48][a]
2008	*Betula pendula, B. pubescens, P. padus, Sorbus aucuparia*	Flowering, vegetative bud burst	Boreal	[49]
2009	*Acer rubrum, Acer saccharinum, Acer saccharum, Aesculus glabra, Carya glabra, Carya ovata, Fraxinus americana, Fraxinus nigra, Juglans nigra, Ostrya virginiana, Pinus contorta, Pinus monticola, Platanus occidentalis, Populus tremuloides, Quercus alba, Quercus bicolor, Quercus macrocarpa, Q. rubra, Quercus velutina, Salix nigra, Sassafras albidum, Ulmus americana*	Leaf unfolding	Temperate	[50]
2012	*B. verrucosa, A. hippocastanum, F. sylvatica, Quercus robus*	Vegetative bud burst	Temperate	[51]
2012	New England vegetation	Remote-sensed start of growing season	Temperate	[52]
2016	*Juglans regia, Prunus armeniaca, Prunus persica*	Flowering, vegetative bud burst	Temperate	[20][b]
2016	*A. hippocastanum, B. pendula, F. sylvatica, L. decidua, P. abies, Q. robur*	Leaf unfolding	Temperate	[53][c]
2017	Vegetation across Northern hemisphere	Remote-sensed start of growing season	Boreal, temperate	[54][c]
2017	*Melia azedarach*	Flowering, leaf unfolding	Subtropical, tropical	[21]
2018	Various[d]	Various[d]	Various	[55][d]

[a]A unifying framework model, data for the indicated six species used as an example.
[b]Empirical data for timing of rest completion included.
[c]Limitations of the inverse modelling discussed.
[d]A programming package for phenology models. Use demonstrated by inverse modelling with the aid of both classical and remote-sensed observational data.

However, in their scenario simulations, Chen *et al.* [21] revealed important implications of the hypothetical rest period and chilling requirement for the studied tree species in the subtropical and tropical conditions. By doing so they pointed out an important gap of knowledge in the ecophysiology of tropical and subtropical trees. Because the modelled hypothetical phenomena had major implications for the projected phenological timing of the examined tree species under climatic change, the phenomena also need to be studied experimentally in tropical and subtropical trees.

Even though the pitfalls inherent in the inverse modelling were revealed 26 years ago [61], as shown by the above discussion, they are unfortunately usually not recognised among the researchers currently carrying out inverse modelling with the process-based tree phenology models. This is indicated by the fact that although various methodological problems are frequently discussed in the inverse modelling publications, the need for experimental studies is usually mentioned only in passing, if at all (Table 1). We are not claiming that the inverse modelling should be stopped once and for all, but at least its limitations should be discussed when publishing the results.

Experimental Designs for Developing Process-Based Tree Phenology Models

Compared with several other physiological processes of plants, the processes underlying the spring phenological events have several peculiarities that hamper their experimental studies. As the physiological basis of rest break is only partially understood (Figure 1A), it goes without saying that it is difficult, if not impossible, to measure its progress directly. The ontogenetic development during quiescence can be observed with microscopic studies (Figure 1B), but compared, for instance, with measurements of growth or gas exchange in plants, the microscopic studies are tedious and time consuming [36,37,63].

However, both rest break and ontogenetic development can be studied indirectly with specific experimental designs where only the occurrence and timing of the phenological event, such as bud burst, is observed [24,38]. This research is based on the hypothetico-deductive method (HDM) widely used in other fields of science for studying phenomena that cannot be observed directly [2]. In that approach, both rest break and ontogenetic development are addressed as nonobservable phenomena, implying that rather than based on direct observations of the processes, the models describing the processes are developed and tested by comparing their predictions for the modelled end point of the processes (bud burst) with observations [2].

The existence and extent of the chilling requirement is studied with a standard chilling–forcing experiment, where the experimental seedlings (or twigs) are first subjected to a chilling treatment of varying duration and after that to a regrowth test in growth-promoting forcing (high temperature) conditions (Figure 2A). If the studied species has the rest period and the chilling requirement, then the bud burst percentage (BB%) increases, and/or the days to bud burst (DBB) in the forcing conditions decreases with increasing duration of chilling [2]. The chilling requirement is then quantified as the duration of chilling (Δt) required for meeting a specific criterion set with the aid of the two variables addressed (Figure 2A).

The chilling requirement of various woody plant species has been studied with experiments such as the one described in Figure 2A in countless studies. However, as a rule those studies do not provide the necessary information for the process-based modelling. Rather, in order to determine the air temperature response of rest break (Figure 1C), the experiment described in Figure 2A needs to be carried out in several constant chilling temperatures, thus obtaining the
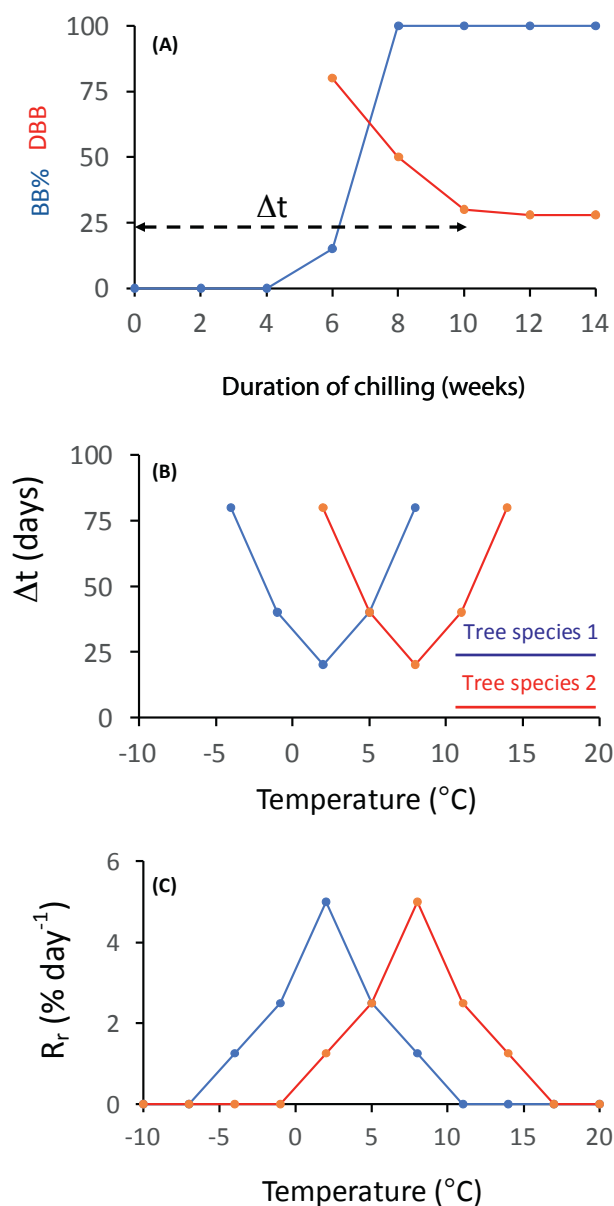
CellPress
REVIEWS

Figure 2. Experimental Design for Determining the Air Temperature Response of Rate of Rest Break, R_r. (A) The principle of the chilling-forcing experiment used in studies of chilling requirement of rest break. Samples of the experimental twigs or seedlings are transferred at intervals from chilling conditions to a regrowth test in forcing (high temperature) conditions, promoting bud burst. In the regrowth test, occurrence and timing of bud burst is observed and the values of two variables are determined for each transfer: Bud burst percentage (BB%; blue line), and days required to bud burst in the forcing conditions [days to bud burst (DBB; red line)]. The duration of chilling required for rest completion, Δt, is determined based on the values of BB% and/or DBB. One option for the determination is shown in the figure. (B) The duration of chilling required for rest completion, Δt, obtained in 11 constant temperatures for two hypothetical tree species. It was assumed that in the lowest and highest temperatures the criterion for rest completion presented in (A) was not met. (C) The air temperature response of rate of rest break in the two hypothetical tree species based on the results in (B). The rate is calculated as the reciprocal of Δt multiplied by 100, and is defined as zero if the criterion set for rest completion was not met [2].

value of Δt for each of them (Figure 2B) [37]. Then, the rate of rest break in any given constant air temperature is calculated as the reciprocal of Δt multiplied by 100 [2], and by combining the values obtained for the different temperatures, the air temperature response of rate of rest break is obtained (Figure 2C). Applying the principle of HDM, the model obtained in controlled constant air temperature conditions is subsequently tested by carrying out the chilling treatment in natural conditions under fluctuating temperatures. If the model obtained in controlled conditions is biologically realistic, then by definition the criterion established for rest completion (Figure 2A) is met in the experiment with fluctuating temperatures at the time when the value of the state of rest break, that is, the sum of the daily values of rate of rest break (Figure 2C), attains

100% [2]. If the model prediction fails in the test, then the result suggests that the process of rest break cannot be modelled realistically by a single air temperature response, so that more complicated model structures, addressing the effects of temperature fluctuation, must be applied [64,65].

Following a similar HDM approach, the air temperature response of rate of ontogenetic development (Figure 1D) is obtained by observing the time required for bud burst of fully chilled seedlings or twigs under different constant air temperatures, calculating the rate as the reciprocal of the time required for bud burst in each constant air temperature multiplied by 100, and plotting the rate values as a function of the experimental temperature [2,36,37]. Similar to the models developed for rest break, the model of ontogenetic development obtained in controlled constant temperatures is tested with the aid of observations in naturally fluctuating temperatures [36,37]. If the model is sufficiently realistic, then bud burst will occur when the sum of the daily values of rate of ontogenetic development (Figure 2C) attains the value of 100%.

Finally, the models for ontogenetic competence can also be tested with the HDM approach by observing only the occurrence and timing of bud burst in a chilling–forcing experiment. This is because the predictions of the sequential and the parallel model for BB% and DBB in the experiment are different (p. 89 in Hänninen [2]).

The experimental designs for applying HDM in developing and testing process-based tree phenology models have been known for a long time, but they are only rarely applied. This is unfortunate, because minor differences in the ecophysiological responses of the processes may cause major differences to the projected effects of climatic change [2,66]. As an example, consider the air temperature response of rate of rest break (Figure 2C). In mild temperate climates, Species 1 would probably experience insufficient chilling under climatic warming, while Species 2, which has a higher range of effective chilling temperatures, would probably have its chilling requirement met also in the warmer climate of the future [67].

It goes without saying that the experimental approach is further improved when the microscopic processes of ontogenetic development during quiescence leading to the visible phenological event are examined directly. In his classical experiments on the effects of air temperature on the rate of ontogenetic development during quiescence, Sarvas [36,37] examined the effects of air temperature on the rate of progress of meiosis in the pollen mother cells in the flower buds of several tree species. Viherä-Aarnio *et al.* [63] applied microscopic observations prior to bud burst in their study addressing the springtime development of vegetative buds of *Picea abies*. By observing the growth of the primordial shoot in the buds as an indicator of ontogenetic development (Figure 1B), they were able to obtain much additional information on bud development before the occurrence of the visible bud burst. They related their findings quantitatively to both chilling and forcing temperatures, thus demonstrating the usefulness of the microscopic studies for the process-based tree phenology modelling. Recently, Chuine *et al.* [20] determined the rest completion of *Prunus armeniaca* in field conditions by observing the changes of the floral primordia fresh weight. They concluded this method considerably facilitated the process-based modelling of phenology in that species.

The few examples discussed above already demonstrate the usefulness of the microscopic observations for process-based tree phenology modelling. It is less clear to what extent measurements of the physiological and molecular phenomena in the buds would currently facilitate the modelling. However, considering the recent advances in understanding the

molecular and physiological basis of rest break and ontogenetic development [31–34], the possibilities of using physiological and molecular phenomena as the basis of the process-based phenological modelling should be addressed in the future. For instance, if quantitative molecular markers for the progress of rest break would be available, then the experiments addressing environmental responses of rest break could be carried out without the time-consuming regrowth tests (Figure 2). Markers for bud **dormancy** were developed several years ago [68,69], but to our knowledge none of the markers developed so far provides the information for the quantitative changes in the ontogenetic competence of the buds, as manifested in the changes of the air temperature response of rate of ontogenetic development during rest period (Figure 1D). Until such quantitative markers are available, the rather tedious and time-consuming regrowth test will be the main approach for model development and testing.

For the sake of simplicity, in this article we focused on the temperature responses of rest break and ontogenetic development (Figure 1C,D). The role of night length (or photoperiod) in regulating the spring phenology of trees is debated in the literature [29,70–73], so its potential effects in any particular tree species need also to be examined with specific experiments designed for that purpose. Other important phenomena to be included in the models with the aid of experimental research include, but are not restricted to, the following: timing of rest initiation, effects of temperature conditions during dormancy induction on the chilling and high temperature requirements, effects of other environmental factors (such as nutrients and drought), and the changes of the environmental responses taking place as the trees get older [2].

Concluding Remarks and Future Perspectives

Here we have demonstrated that despite being straightforward and relatively easy to implement, the currently popular inverse modelling does not provide a shortcut to biologically realistic process-based models of tree phenology. Rather, time-consuming experimental work is needed for the development of realistic models. The good news is that experimental designs for developing and testing the models are readily available. This provides a solid methodological basis for well-coordinated cooperation between climatic change modellers and tree ecophysiologists. In order to promote trustworthy assessing of the ecological effects of climatic change, we are calling for such cooperation (see Outstanding Questions).

Author Contributions

H.H. and K.R. had the main responsibility in writing the text. K.T., R.Z., J.W., and Y.H.F. commented several times on the draft.

Disclaimer Statement

The authors declare no competing financial interests.

References

1. Heide, O.M. *et al.* (1985) Physiological aspects of climatic adaptation in plants with special reference to high-latitude environments. In *Plant Production in the North* (Kaurin, Å., ed.), pp. 1–22, Norwegian University Press

Outstanding Questions

How do environmental factors regulate rest break and ontogenetic development towards bud burst in different tree species and provenances? In order to project the effects of climatic warming with computer simulations, exact quantitative environmental responses need to be established with experimental research.

What is the role of night length (photoperiod) in regulating the rest break and ontogenetic development towards bud burst in different tree species and provenances? Concerning the partially conflicting conclusions in the literature, more experimental research is needed to clarify this.

Do subtropical tree species and provenances have rest period and chilling requirement of rest completion?

How does climate change affect the timing of bud burst in different boreal, temperate, and subtropical tree species in different climatic conditions? This question can be readily addressed with computer simulations, once realistic process-based tree phenology models have been developed with the aid of experimental research.

2. Hänninen, H. (2016) *Boreal and Temperate Trees in a Changing Climate: Modelling the Ecophysiology of Seasonality,* Springer

3. Keeling, R.F. *et al.* (1996) Global and hemispheric CO_2 sinks deduced from changes in atmospheric O_2 concentration. *Nature* 381, 218–221

4. Kramer, K. and Hänninen, H. (2009) The annual cycle of development of trees and process-based modelling of growth to scale up from the tree to the stand. In *Phenology of Ecosystem Processes* (Noormets, A., ed.), pp. 201–227, Springer

5. Richardson, A.D. *et al.* (2010) Influence of spring and autumn phenological transitions on forest ecosystem productivity. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 365, 3227–3246

6. Visser, M.E. and Holleman, L.J. (2001) Warmer springs disrupt the synchrony of oak and winter moth phenology. *Proc. R. Soc. Lond. B Biol. Sci.* 268, 289–294

7. Memmott, J. *et al.* (2007) Global warming and the disruption of plant–pollinator interactions. *Ecol. Lett.* 10, 710–717

8. Wolf, R. (2008) *The Easter Freeze of April 2007: A Climatological Perspective and Assessment of Impacts and Services*. Technical Report 2008-01, NOAA/USDA

9. Richardson, A.D. *et al.* (2018) Ecosystem warming extends vegetation activity but heightens vulnerability to cold temperatures. *Nature* 560, 368–371

10. Myneni, R.B. *et al.* (1997) Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature* 386, 698–702

11. Menzel, A. and Fabian, P. (1999) Growing season extended in Europe. *Nature* 397, 659

12. Menzel, A. *et al.* (2006) European phenological response to climate change matches the warming pattern. *Glob. Change Biol.* 12, 1969–1976

13. Linkosalo, T. *et al.* (2009) The time series of flowering and leaf bud burst of boreal trees (1846-2005) support the direct temperature observations of climatic warming. *Agric. Forest Meteorol.* 149, 453–461

14. Yu, H. *et al.* (2010) Winter and spring warming result in delayed spring phenology on the Tibetan Plateau. *Proc. Natl. Acad. Sci. U. S. A.* 107, 22151–22156

15. Laube, J. *et al.* (2014) Chilling outweighs photoperiod in preventing precocious spring development. *Glob. Change Biol.* 20, 170–182

16. Fu, Y.H. *et al.* (2015) Declining global warming effects on the phenology of spring leaf unfolding. *Nature* 526, 104–107

17. Chen, L. *et al.* (2018) Spring phenology at different altitudes is becoming more uniform under global warming in Europe. *Glob. Change Biol.* 24, 3969–3975

18. Ma, Q. *et al.* (2018) Reduced geographical variability in spring phenology of temperate trees with recent warming. *Agric. Forest Meteorol.* 256–257, 526–533

19. Murray, M.B. *et al.* (1989) Date of budburst of fifteen tree species in Britain following climatic warming. *J. Appl. Ecol.* 26, 693–700

20. Chuine, I. *et al.* (2016) Can phenological models predict tree phenology accurately in the future? The unrevealed hurdle of endodormancy break. *Glob. Change Biol.* 22, 3444–3460

21. Chen, X. *et al.* (2017) Delayed response of spring phenology to global warming in subtropics and tropics. *Agric. Forest Meteorol.* 234, 222–235

22. Hänninen, H. and Tanino, K. (2011) Tree seasonality in a warming climate. *Trends Plant Sci.* 16, 412–416

23. Lang, G.A. *et al.* (1987) Endo-, para-, and ecodormancy: physiological terminology and classification for dormancy research. *HortScience* 22, 371–377

24. Hänninen, H. (1990) Modelling bud dormancy release in trees from cool and temperate regions. *Acta For. Fenn.* 213, 1–47

25. Hannerz, M. *et al.* (2003) Variation in chilling requirements for completing bud rest between provenances of Norway spruce. *Silvae Genet.* 52, 161–168

26. Heide, O.M. (1993) Dormancy release in beech buds (*Fagus sylvatica*) requires both chilling and long days. *Physiol. Plant.* 89, 187–191

27. Caffarra, A. and Donnelly, A. (2011) The ecological significance of phenology in four different tree species: effects of light and temperature on bud burst. *Int. J. Biometeorol.* 55, 711–721

28. Basler, D. and Körner, Ch. (2012) Photoperiod sensitivity of bud burst in 14 temperate forest tree species. *Agric. Forest Meteorol.* 165, 73–81

29. Vitasse, Y. and Basler, D. (2013) What role for photoperiod in the bud burst phenology of European beech. *Eur. J. Forest Res.* 132, 1–8

30. Coville, F.V. (1920) The influence of cold in stimulating the growth of plants. *J. Agric. Res.* 20, 151–160

31. Cooke, J.E.K. *et al.* (2012) The dynamic nature of bud dormancy in trees: environmental control and molecular mechanisms. *Plant Cell Environ.* 35, 1707–1728

32. Kudoh, H. (2016) Molecular phenology in plants: *in natura* systems biology for the comprehensive understanding of seasonal responses under natural environments. *New Phytol.* 210, 399–412

33. Zhang, Z. *et al.* (2018) Transcriptome profiles reveal the crucial roles of hormone and sugar in the bud dormancy of *Prunus mume*. *Sci. Rep.* 8, 5090

34. Tylewicz, S. *et al.* (2018) Photoperiodic control of seasonal growth is mediated by ABA acting on cell-cell communication. *Science* 360, 212–215

35. Chuine, I. *et al.* (2013) Plant development models. In *Phenology: An Integrative Environmental Science* (2nd edn) (Schwartz, M.D., ed.), pp. 275–293, Springer

36. Sarvas, R. (1972) Investigations on the annual cycle of development of forest trees: Active period. *Commun. Inst. For. Fenn.* 76, 1–110

37. Sarvas, R. (1974) Investigations on the annual cycle of development of forest trees. II. Autumn dormancy and winter dormancy. *Commun. Inst. For. Fenn.* 84, 1–101

38. Fuchigami, L.H. *et al.* (1982) A degree growth stage (°GS) model and cold acclimation in temperate woody plants. In *Plant Cold Hardiness and Freezing Stress. Mechanisms and Crop Implications.* (Vol. 2) (Li, P.H. and Sakai, A., eds), pp. 93–116, Academic Press

39. Alberto, F.J. *et al.* (2013) Potential for evolutionary responses to climate change – evidence from tree populations. *Glob. Change Biol.* 19, 1645–1661

40. Hänninen, H. and Kramer, K. (2007) A framework for modelling the annual cycle of trees in boreal and temperate regions. *Silva Fenn.* 41, 167–205

41. Chuine, I. and Régnière, J. (2017) Process-based models of phenology for plants and animals. *Annu. Rev. Ecol. Evol. Syst.* 48, 159–182

42. Hänninen, H. and Lundell, R. (2007) Dynamic models in plant ecophysiology. In *Physiology of Northern Plants under Changing Environment* (Taulavuori, E. and Taulavuori, K., eds), pp. 157–175, Research Signpost

43. Aster, R. *et al.* (2013) *Parameter Estimation and Inverse Problems.* (2nd edn) Elsevier

44. Kramer, K. (1994) Selecting a model to predict the onset of growth of *Fagus sylvatica*. *J. Appl. Ecol.* 31, 172–181

45. Kramer, K. (1994) A modelling analysis of the effects of climatic warming on the probability of spring frost damage to tree species in The Netherlands and Germany. *Plant Cell Environ.* 17, 367–377

46. Chuine, I. *et al.* (1998) Fitting models predicting dates of flowering of temperate-zone trees using simulated annealing. *Plant Cell Environ.* 21, 455–466

47. Chuine, I. *et al.* (1999) Selecting models to predict the timing of flowering of temperate trees: implications for tree phenology modelling. *Plant Cell Environ.* 22, 1–13

48. Chuine, I. (2000) A unified model for budburst of trees. *J. Theor. Biol.* 207, 337–347

49. Linkosalo, T. *et al.* (2008) A comparison of phenological models of leaf bud burst and flowering of boreal trees using independent observations. *Tree Physiol.* 28, 1873–1882

50. Morin, X. *et al.* (2009) Leaf phenology in 22 North American tree species during the 21st century. *Glob. Change Biol.* 15, 961–975

51. Fu, Y.H. *et al.* (2012) Bayesian comparison of six different temperature-based budburst models for four temperate tree species. *Ecol. Model.* 230, 92–100

52. Yang, X. *et al.* (2012) Regional scale phenology modelling based on meteorological records and remote sensing observations. *J. Geophys. Res.* 117, G03029

53. Basler, D. (2016) Evaluating phenological models for the prediction of leaf-out dates in six temperate tree species across central Europe. *Agric. Forest Meteorol.* 217, 10–21

54. Liu, Q. *et al.* (2017) Simulating the onset of spring vegetation growth across the Northern Hemisphere. *Glob. Change Biol.* 2018; 24, 1342–1356

55. Hufkens, K. *et al.* (2018) An integrated phenology modelling framework in R. *Methods Ecol. Evol.* 9, 1276–1285

56. Templ, B. *et al.* (2018) Pan European phenological data base (PEP725): a single point of access for European data. *Int. J. Biometeorol.* 62, 1109–1113

57. Wolkovich, E.M. *et al.* (2016) Warming experiments underpredict plant phenological responses to climate change. *Nature* 485, 494–497

58. Levins, R. (1966) The strategy of model building in population biology. *Am. Sci.* 54, 421–431

59. Levins, R. (1968) *Evolution in Changing Environments. Some Theoretical Explorations,* Princeton University Press

60. Sharpe, P.J.H. *et al.* (1990) Forest modeling approaches: compromises between generality and precision. In *Process Modeling of Forest Growth Responses to Environmental Stress* (Dixon, R. K., ed.), pp. 180–190, Timber Press

61. Hunter, A.F. and Lechowicz, M.J. (1992) Predicting the timing of budburst in temperate trees. *J. Appl. Ecol.* 29, 597–604

62. Hänninen, H. (1995) Effects of climatic change on trees from cool and temperate regions: an ecophysiological approach to modelling of bud burst phenology. *Can. J. Bot.* 73, 183–199

63. Viherä-Aarnio, A. *et al.* (2014) Internal development of vegetative buds of Norway spruce trees in relation to accumulated chilling and forcing temperatures. *Tree Physiol.* 34, 547–556

64. Fishman, S. *et al.* (1987) The temperature dependence of dormancy breaking in plants: mathematical analysis of a two-step model involving a cooperative transition. *J. Theor. Biol.* 124, 473–483

65. Fishman, S. *et al.* (1987) The temperature dependence of dormancy breaking in plants: computer simulation of processes studied under controlled temperatures. *J. Theor. Biol.* 126, 309–321

66. Hänninen, H. (2006) Climate warming and the risk of frost damage to boreal forest trees: identification of critical ecophysiological traits. *Tree Physiol.* 26, 889–898

67. Tanino, K.K. and Wang, R. (2008) Modeling chilling requirement and diurnal temperature differences on flowering and yield performance in strawberry crown production. *HortScience* 43, 2060–2065

68. Rinne, P.L.H. *et al.* (2016) Axillary buds are dwarfed shoots that tightly regulate GA pathway and GA-inducible 1,3-β-glucanase genes during branching in hybrid aspen. *J. Exp. Bot.* 67, 5975–5991

69. Svendsen, E. *et al.* (2016) A molecular marker associated with low-temperature induction of dormancy in red osier dogwood (*Cornus sericea*). *Tree Physiol.* 27, 385–397

70. Körner, Ch. and Basler, D. (2010) Phenology under global warming. *Science* 327, 1461–1462

71. Körner, Ch. and Basler, D. (2010) Response. *Science* 329, 278

72. Chuine, I. *et al.* (2010) Warming, photoperiods, and tree phenology. *Science* 329, 277–278

73. Zohner, M. *et al.* (2016) Day length unlikely to constrain climate-driven shifts in leaf-out times of northern woody plants. *Nat. Clim. Change* 6, 1120–1123